Topographic History of the Maui Nui Complex, Hawai'i, and Its Implications for Biogeography[1]

Jonathan Paul Price[2,4] and Deborah Elliott-Fisk[3]

Abstract: The Maui Nui complex of the Hawaiian Islands consists of the islands of Maui, Moloka'i, Lāna'i, and Kaho'olawe, which were connected as a single landmass in the past. Aspects of volcanic landform construction, island subsidence, and erosion were modeled to reconstruct the physical history of this complex. This model estimates the timing, duration, and topographic attributes of different island configurations by accounting for volcano growth and subsidence, changes in sea level, and geomorphological processes. The model indicates that Maui Nui was a single landmass that reached its maximum areal extent around 1.2 Ma, when it was larger than the current island of Hawai'i. As subsidence ensued, the island divided during high sea stands of interglacial periods starting around 0.6 Ma; however during lower sea stands of glacial periods, islands reunited. The net effect is that the Maui Nui complex was a single large landmass for more than 75% of its history and included a high proportion of lowland area compared with the contemporary landscape. Because the Hawaiian Archipelago is an isolated system where most of the biota is a result of in situ evolution, landscape history is an important determinant of biogeographic patterns. Maui Nui's historical landscape contrasts sharply with the current landscape but is equally relevant to biogeographical analyses.

The Hawaiian Islands present an ideal setting in which to weigh the relative influences of ecological phenomena (concerned with local conditions and species interactions) and historical phenomena (concerned with dispersal and speciation) on the composition of species assemblages. Environmental gradients such as elevation and moisture are very readily studied in the Hawaiian Islands, as compared with many regions. The Islands also span a remarkable time line of geologic histories that can be reconstructed more easily and accurately than in most regions. Having been extremely isolated in the Pacific since its inception, the Hawaiian biota has evolved in situ from a limited number of colonists, achieving very high levels of endemism (Carlquist 1980). Hawai'i's biota is therefore best examined in terms of how current conditions and island history relate to the dispersal, evolution, and extinction of organisms.

The Hawaiian Islands are volcanic in origin, going through a life cycle with well-defined stages (Macdonald and Abbott 1970, Moore and Clague 1992). Upon formation on the seafloor, a volcano grows until it forms a gently sloped volcanic shield above the sea surface. During shield building and for some time after completion, weight of the volcanic mass on Earth's crust causes it to subside. Despite some postshield volcanism, subsequent erosion and subsidence further reduce the volcano to sea level until it ultimately becomes an atoll or seamount. Volcanoes of the Hawaiian Archipelago increase in age to the northwest, exhibiting a linear progression of

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[2] Department of Botany, MRC-166, National Museum of Natural History, Smithsonian Institution, P.O. Box 37012, Washington, D.C. 20013-7012.

[3] Department of Wildlife, Fisheries, and Conservation Biology, University of California, Davis, 1 Shields Avenue, Davis, California 95616.

[4] Corresponding author.

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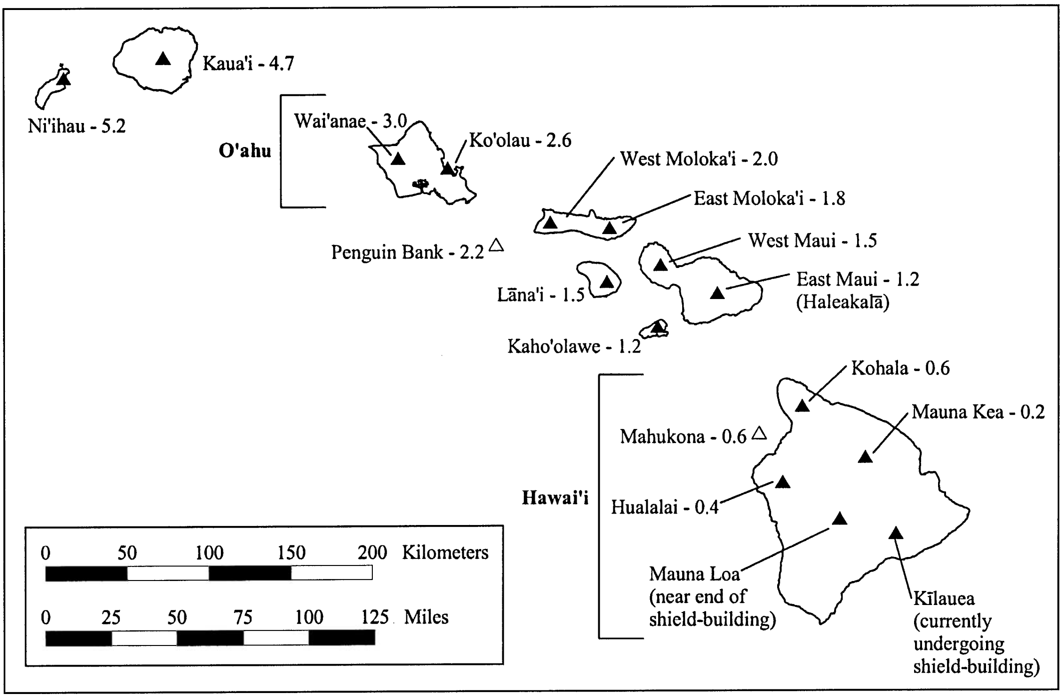

FIGURE 1. Volcanoes of the major Hawaiian Islands. Ages given in myr are from Clague (1996) and reflect the estimated end of the shield-building stage.

these stages (Figure 1). Although this age gradient is the primary historical variable, the islands of Maui, Moloka‘i, Lāna‘i, and Kaho‘olawe share a distinct history in having once formed a single island, "Maui Nui."

Stearns and Macdonald (1942) first suggested that four islands of the Maui Nui complex were conjoined before subsidence. Age and duration of this formation remained vague, however. Later understanding of sea-level history and bathymetry surrounding the Islands revealed that they were connected recently during the low sea stands of glacial periods into a landmass referred to as "Maui Nui," Hawaiian for "Big Maui" (Macdonald and Abbott 1970, Nullet et al. 1998). Detailed bathymetry and marine geological exploration made possible by submersible vehicles illuminated the magnitude of subsidence: areas surrounding the Islands have subsided as much as 2000 m as evidenced by former shoreline features existing at extreme depths (Moore 1987). The only estimate of the nature and timing of changes in Maui Nui's configuration due to subsidence is that by Carson and Clague (1995). They postulated the following sequence: (1) Penguin Bank Volcano was connected to the island of O‘ahu via a land bridge; (2) newer volcanoes in the Maui Nui complex coalesced with older ones, ultimately forming a single landmass larger than the current island of Hawai‘i; (3) as subsidence ensued, submerging saddles between its volcanoes, this landmass gradually divided into separate islands as Moloka‘i/Lāna‘i separated from Maui/Kaho‘olawe less than 300,000 to 400,000 years ago (ka); and (4) finally, the complex consisted of four discrete islands by less than 100 to 200 ka. However, concurrent with these events, sea-level changes reunited the fragments periodically, as pointed out by Asquith (1995). Thus, multiple processes have resulted in a complex history.

Our current understanding of volcanism, subsidence, and sea-level change, along with advances in submarine surveying and available Geographic Information System (GIS) technology, makes possible a detailed reconstruction of how the spatial and topographic characteristics of the Maui Nui complex have changed over time. Also, because climate in the Hawaiian Islands is largely a function of topographic attributes of an island (e.g., height of mountain masses, aspect with respect to weather systems), details of past topographic attributes should help resolve climate history, thus further enhancing understanding of evolutionary history. The complex history presented here provides a framework on which to base detailed biogeographical hypotheses.

MATERIALS AND METHODS

The first step in modeling past landscapes of the Maui Nui complex is accurate compilation of geographic data. Topographic and bathymetric (seafloor topography) data were obtained from several sources. High-precision sonar data were supplied by James Gardner (U.S. Geological Survey, Menlo Park, California) and David Clague (Monterey Bay Aquarium Research Institute, Moss Landing, California). A less detailed but more spatially extensive composite data set came from the University of Hawai'i, School of Ocean and Earth Science and Technology. This was used for areas where detailed sonar data were unavailable or had sparse coverage, as well as for all areas above sea level. The area between Moloka'i and Lāna'i was not accurately represented by any data set, and so spot depths from a National Oceanic and Atmospheric Administration nautical chart were used; the lower precision of these data is acceptable given the shallow depth of the area (<100 m), which makes them sufficiently accurate. In scattered locations, elevations were interpolated from nearby data in small areas where no accurate data were available. All data to be used were compiled into a digital elevation model (DEM) using the GIS software ArcInfo (Environmental Systems Research Institute 1999). This consisted of a grid of values representing the elevation at each point, the resolution (lateral spacing of points) of which was 300 m.

Key features were identified from this base DEM in conjunction with published sources and consultation with geologists (David Clague, David Sherrod). These features, including former shorelines and volcanic features, defined five components of a composite model, each detailing a given physical characteristic or process. The major components of the model are as follows: (1) assessment of age and spatial distribution of volcanic shields; (2) reconstruction of East Maui's (Haleakalā Volcano) topography before and after extensive postshield volcanism; (3) estimation of the extent and timing of major erosion and landslides; (4) determination of the timing and spatial variability of tectonic subsidence; and (5) consideration of glacioeustatic sea-level change. The overall model adjusts the base DEM by accounting for the processes in each component to create new DEMs approximating the topography of the Maui Nui complex through time. Each component is detailed here.

Shield-Building Volcanism

Volcanoes in the Hawaiian Islands form in response to hot-spot magmatism deep below the lithosphere. As a volcano is moved away from the hot spot by motion of the Pacific tectonic plate, it ceases volcanic activity and a new vent forms (Wilson 1963). Thus a chain of volcanoes forms along the direction of plate motion, with younger volcanoes near the position of the hot spot. As volcanoes emerge above the sea surface, they form a gently sloping volcanic shield composed of tholeiitic basalt. The period from when a new volcano breaks the sea surface to the end of shield building is estimated to last between about 0.5 million yr (myr) (Moore and Clague 1992) and 1.0 myr (Guillou et al. 2000). Available radiometric ages of tholeiitic lavas come from different points within this stage, including some that may have been emplaced long after the majority of a shield edifice had been constructed. We have chosen to use Clague's (1996) age estimates, derived from an empirical model based on the most reliable radiometric dates, because they represent approximations of when the bulk of each shield's mass had accumulated. We therefore refer to shield building as a structural, rather than a mineralogical, phase. Because volcanoes experience a sequence of tectonic, volcanic, and geomorphic processes after shield formation, this age is a reference point for the initiation of that sequence.

The seven volcanoes of the Maui Nui complex completed shield building between 2.2 million yr ago (Ma) for Penguin Bank Volcano and 1.2 Ma for Haleakalā and Kahoʻolawe Volcanoes. Because each volcanic shield overlies large parts of previously formed volcanoes, it is impossible to reconstruct the shapes of volcanic surfaces that have been covered. A detailed and quantitative model can only encompass the time after Haleakalā and Kahoʻolawe Volcanoes (the youngest in the complex) completed shield building (1.2 Ma), with the prior history being general and descriptive. The 1.2-myr age is probably well substantiated for Haleakalā, because reliably dated subaerial shield or early postshield lavas (Honomanū Volcanics [Stearns and Macdonald 1942]) are as old as 1.1 myr (Chen et al. 1991). For Kahoʻolawe postshield lavas are as old as 1.15 myr (Fodor et al. 1992).

Late-Stage Volcanism

Eruption of more viscous and explosive alkalic lava (as opposed to free-flowing tholeiitic lava) after the main shield-building stage results in more steeply sloped surfaces and the formation of a distinct "alkalic cap" (Stearns and Macdonald 1942). An especially thick cap referred to as the Kula Volcanics surmounts the summit region of Haleakalā Volcano (Figures 2, 3). Projecting the outer slopes of Haleakalā to where the summit existed before erosion, the alkalic cap probably rose to an elevation of 250 m above the current summit, about 3300 m elevation; the actual elevation of the summit at that time was higher because some subsidence has occurred since then (see Subsidence later in this section). Using the TopoGrid interpolation

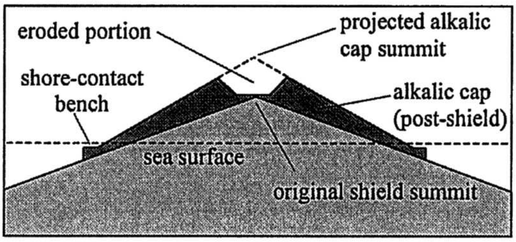

FIGURE 2. Shield building and postshield (alkalic cap) formation. This conceptual profile represents the major features of Haleakalā Volcano: the original gently sloped tholeiitic shield, the steeply sloped alkalic cap with shore contact bench marking its lower extent, and the summit crater (eroded portion of the cap). Compare with Figure 3.

function in ArcInfo, a DEM representing the estimated topography of the uneroded alkalic cap was constructed. This function creates DEMs from multiple point and contour data sources; inputs used in this interpolation included the estimated summit elevation and position, topography of the uneroded portions of the cap, and a few "guide" contour lines that project the shape of the surface where it has been deeply eroded. The product of this interpolation is a reconstruction of the alkalic cap before it eroded.

The approximate shape of the underlying shield of Haleakalā can be estimated because the thickness of the alkalic cap can be ascertained in a few locations. In the vicinity of the Maui isthmus, the alkalic cap is estimated to be less than 100 m thick based on drill cores (Stearns and Macdonald 1942). In Honomanū Gulch, where erosion has exposed late shield or transitional lavas called Honomanū Volcanics, the cap is perhaps 300 m thick. In the vicinity of the summit (which has been deeply incised, forming Haleakalā Crater), lavas at the base of the exposed portion of the cap formed about 0.9 Ma (Sherrod et al. 2003) and therefore are nearly as old as the Honomanū Volcanics. Therefore the original shield summit was likely not far below the bottom of Haleakalā Crater, probably around 2000 m current elevation; the actual elevation of the shield summit at its formation was higher because considerable subsidence has occurred since that time (about 1.2 Ma). With

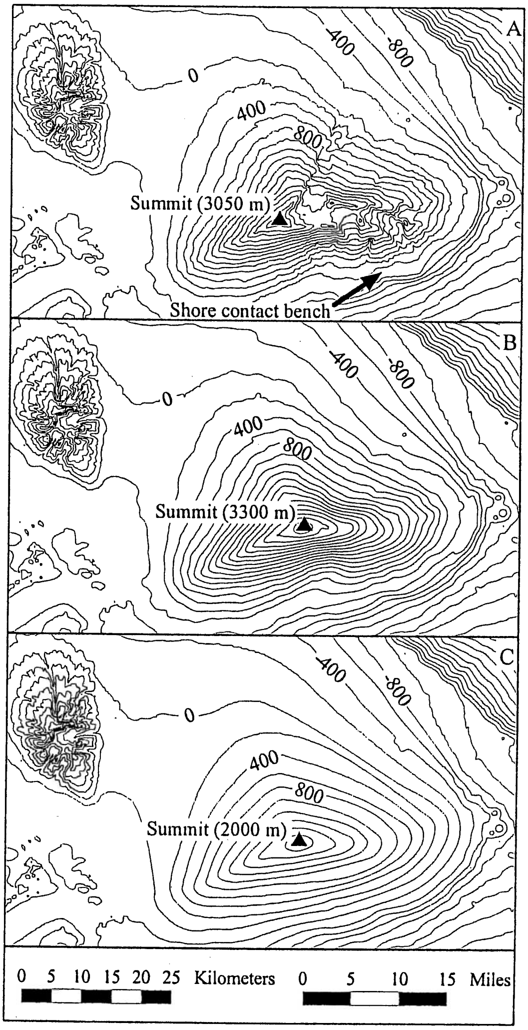

FIGURE 3. Map of changing topography of Haleakalā summit. Contour interval 200 m. *A*, Current topography; *B*, reconstructed alkalic cap (0.4 Ma); *C*, estimated original tholeiitic shield (1.2 Ma). These models represent elevation relative to present and do not account for tectonic subsidence. Changes in bathymetry/topography outside the extent of the alkalic cap are not considered.

the alkalic cap summit at 3300 m and the original shield summit at 2000 m elevation, the thickness of the alkalic cap around the summit was about 1300 m. Therefore the alkalic cap is thickest near the summit and gradually thinner with greater distance from the summit. Because lava cools quickly when it contacts the shore, a bench marks the lower edge of the alkalic cap. Below the base of this bench, slopes are more modest and probably represent the shape of the original tholeiitic shield because the alkalic cap is probably thin this far from the summit. Again, using the TopoGrid interpolater, a DEM representing the original shape of the shield was created. Confining the interpolation to the estimated area of the alkalic cap, inputs included the estimated position and elevation of the shield summit and "guide" contour lines representing projected slopes, based on slopes below the base of the cap.

The bulk of Haleakalā's alkalic cap had formed by about 0.4 Ma, after which volcanic activity slowed dramatically (Sherrod et al. 2002). For the sake of simplicity, a linear growth function for the alkalic cap was used. This entailed creating intermediate DEMs whose elevation values were calculated as a linear transition from the original shield 1.2 Ma to the fully formed alkalic cap 0.4 Ma. Thus, the rate of vertical growth at the summit is estimated to have been 1300 m in 0.8 myr, or 1.6 mm/yr, and slower toward the edges of the cap, where volcanic deposition was less. Adjusted DEMs were calculated at intervals of 0.01 myr (10,000 yr) during that period. Again, this growth in the summit region was countered by subsidence, which entails further adjustment of the DEM (discussed later).

Erosion and Landslides

Over long time periods, erosion is an important factor in changing the topography of an island. Erosion is difficult to model because there is no accurate way to determine the timing and magnitude of all events. Most volcanoes in the Maui Nui complex have not undergone erosion substantial enough to greatly alter their original volcanic slopes. Two exceptions to this are East Moloka'i, which experienced a major landslide and subsequent accelerated erosion, and Haleakalā, which, though otherwise intact, experienced rapid and deep erosion of its summit area.

East Moloka'i's topography was altered dramatically by a massive landslide that removed much of the north slope of the volcano (Moore et al. 1989). This likely occurred around the time of the completion of shield building, because canyons that formed above the sea surface after the slope failure extend to considerable depth, having subsided over a long period of time. The creation of an unstable, oversteepened slope probably accelerated erosion, substantially lowering the summit elevation. Although it is possible to estimate the shield's shape before the landslide and subsequent erosion, these events occurred early in the postshield history of East Moloka'i and therefore before the start of the detailed model.

An easily reconstructed scenario exists for Haleakalā Crater, which is an erosional feature. Because lavas were deposited on the outer slopes as recently as 0.15 Ma, there probably was no prominent summit erosional feature at that time, because lavas originating at the summit would have flowed into the crater rather than on the outer slopes. Lavas that flowed out of the summit depression are as old as 0.12 myr (Sherrod et al. 2002). Therefore, there was a very brief period during which the summit likely eroded: before that period, lavas flowed outside the slopes, and after that, lavas flowed into the floor of the depression and down to the coast. Therefore it appears that the crater was formed as a series of catastrophic landslides that continued to incise the summit once an unstable slope was formed. The resulting erosion reduced the summit by 250 m and created a depression 600 m deep. Because the episodic nature of the landslides cannot be dated precisely, modeling this reduction is most simply represented by a linear function. Intermediate DEMs were calculated as a linear transition from the fully formed alkalic cap 0.15 Ma to the elevation values of the base DEM 0.12 Ma at intervals of 0.01 myr.

Subsidence

Throughout the growth of a volcano and for some time after completion of its shield, weight on the thin oceanic crust causes the volcano to subside. During shield building, rapid growth outpaces subsidence and there is a net increase in height and area. However, when shield building ceases, net subsidence submerges many areas formerly above sea level. There are also some circumstances when uplift may occur. When giant landslides remove large portions of a volcano's mass (around the end of shield building), isostatic rebound may occur, resulting in uplift of perhaps up to 100 m (Smith and Wessel 2000). Muhs and Szabo (1994) demonstrated that O'ahu (long past shield building) has recently uplifted at a very low rate due to compensational lithospheric flexure in response to regional subsidence in the vicinity of Hawai'i. Both of these modes of uplift are modest in comparison with the rate and magnitude of subsidence, and probably have occurred little in the Maui Nui complex during the period covered in detail by this model.

A number of subsidence rate estimates are based on examination of recent changes in tide gauge measurements. A 38-yr record from a tide gauge in Hilo, on the currently subsiding island of Hawai'i, indicated a net subsidence rate (after accounting for sea-level change) of 2.4 mm/yr. In Kahului, Maui, the tide gauge indicates very little subsidence (0.3 mm/yr); thus the Haleakalā Volcano (whose age is 1.2 myr) essentially has completed its subsidence stage (Moore 1987).

Tide gauges indicate the rate of subsidence for only one site over a very brief period of time, however. A longer-term estimate has been determined by examining the ages of a series of submerged coral reefs. Campbell (1984) proposed that, on a subsiding surface, coral reefs could only grow during periods when sea level was dropping, because that is the only time that the relative position of the shore remains constant; he derived a rate of subsidence of 2.0 mm/yr based on a uranium-series age of a reef northwest of Hawai'i. Moore and Fornari (1984) used estimates of the timing of low sea stands (Chappell 1983) to assign ages to different coral reefs and then used these ages and the depths of the reefs to derive a subsidence rate of 1.8 to 3.0 mm/yr west of the island of Hawai'i. Moore and Campbell (1987) used similar methods to derive subsidence rates of 2.5 mm/yr northwest of Hawai'i and 3.0 mm/yr west of Lāna'i. The drawback to this method is that the ages of submerged reefs are assumed from sea-level estimates. Because Lāna'i completed shield building around 1.5 Ma, the assigned ages of the nearby reefs at 0.65–0.35 myr are probably too young. Uranium-series radiometric dates of several reefs northwest of Hawai'i yield a subsidence rate of about 2.6 mm/yr (Ludwig et al. 1991). Electron spin resonance dating of reefs between Maui and Hawai'i yield a subsidence rate of 3–4 mm/yr south of Maui (Jones 1995); however, the age estimates for these reefs are too young, considering their depths and the time Haleakalā completed shield building. Thus, the only reliable subsidence rates based on coral reefs are those near Hawai'i, which are comparable with the tide gauge estimate of 2.4 mm/yr.

A rough but long-term estimate of the rate of subsidence can be determined from close examination of a feature referred to as the break-in-slope. Lava extruded underwater is cooled quickly, forming a steep slope, but that extruded subaerially (above the sea surface) cools more slowly, remaining fluid longer and forming more gentle slopes; thus there is a sharp transition between submarine and subaerial lavas, manifested as a break-in-slope, that demarcates the maximum extent of the shoreline before shield building waned and subsidence submerged the feature (Moore 1987). There are several breaks-in-slope associated with volcanoes of different ages. The most notable of these are the H and K terraces associated with Haleakalā (East Maui) and East Moloka'i Volcanoes, respectively (Figure 4) (Moore 1987). These terraces, representing the maximum extents

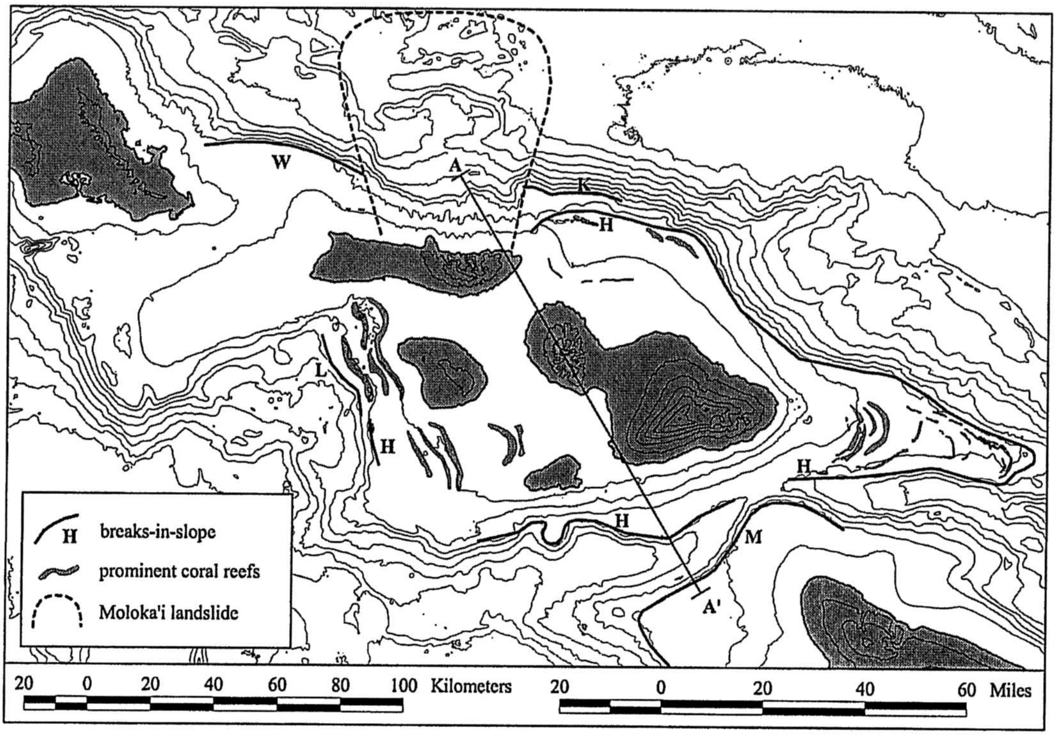

FIGURE 4. Submerged geologic features. Contour interval is 500 m. Heavy lines show approximate location of breaks-in-slope associated with different volcanoes. Gray areas below sea level represent deeply submerged reefs. The dashed line outlines the massive landslide north of Moloka'i. Line A-A′ represents the transect of the profile in Figure 5. The naming convention for different breaks-in-slope (terraces) is as follows: M, Māhukona/Kohala; H, Haleakalā (East Maui); K, East Moloka'i; L, Lāna'i; W, West Moloka'i.

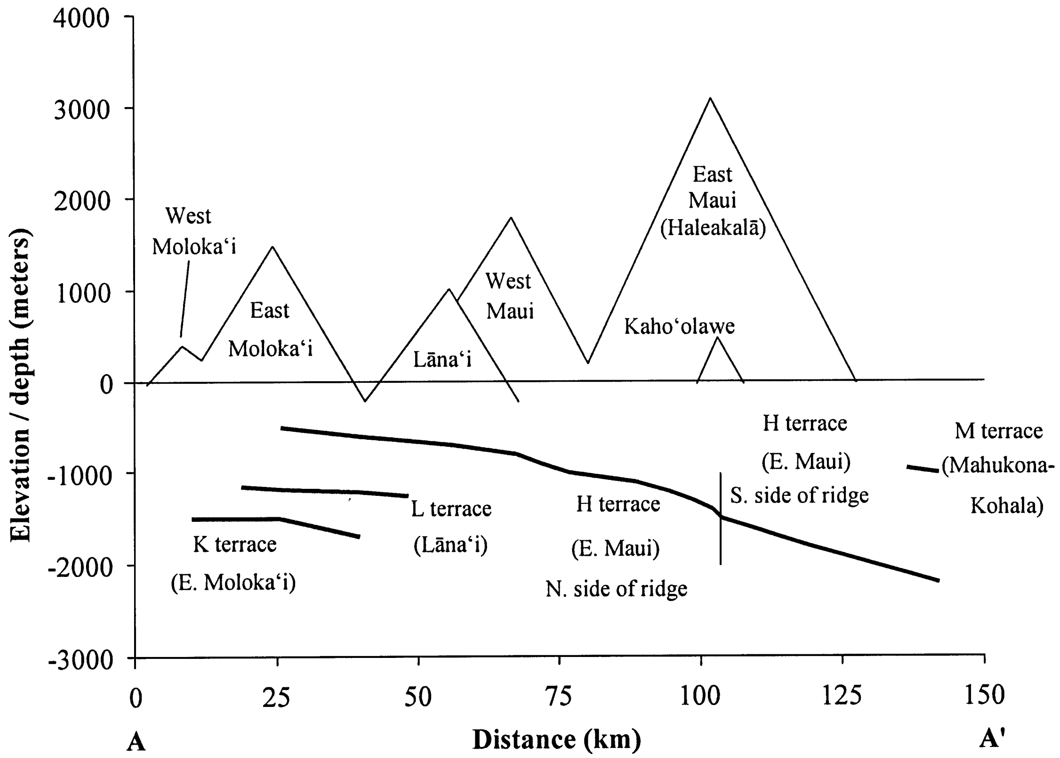

FIGURE 5. Profile of features from Figure 4 projected into vertical plane along transect line A-A′. Vertical exaggeration is 15 times. Major breaks-in-slope indicated by heavy line labeled according to naming convention from Figure 4.

of the shorelines of their associated volcanoes, formed at the end of shield building of each volcano.

An important aspect of subsidence is that it varies spatially. The H terrace is about 500 m deep near Moloka'i but is over 2000 m deep east of Maui, meaning that this originally horizontal feature has tilted as it subsided (Figure 5). This tilt is a function of faster subsidence rates occurring closer to the current zone of volcanic loading and slower rates in areas farther from the hot spot (Moore 1987). The direction of tilt is approximately southeast toward the island of Hawai'i, parallel to the trend of volcanic propagation, except for the Haleakalā Ridge east of Maui, which tilts in a more southerly direction (which is again toward Hawai'i) (Moore et al. 1992). Depth of the H terrace at a given location indicates how much subsidence has occurred since its formation 1.2 Ma. Using these depths, a map was created to show the amount of subsidence that has occurred in different areas since that time by constructing lines of equal subsidence perpendicular to the tilt direction (Figure 6). It is likely that the middle of the ridge subsided more than the edges (where the depth of the H terrace records the amount of subsidence); however, this difference is probably relatively minor and cannot be determined accurately. The assumed iso-subsidence lines were interpolated into a grid of gradually varying values representing how much subsidence has occurred at a given grid location since 1.2 Ma ("subsidence amount grid"). By simply adding this grid of values to the adjusted DEM representing the original shield, the H terrace

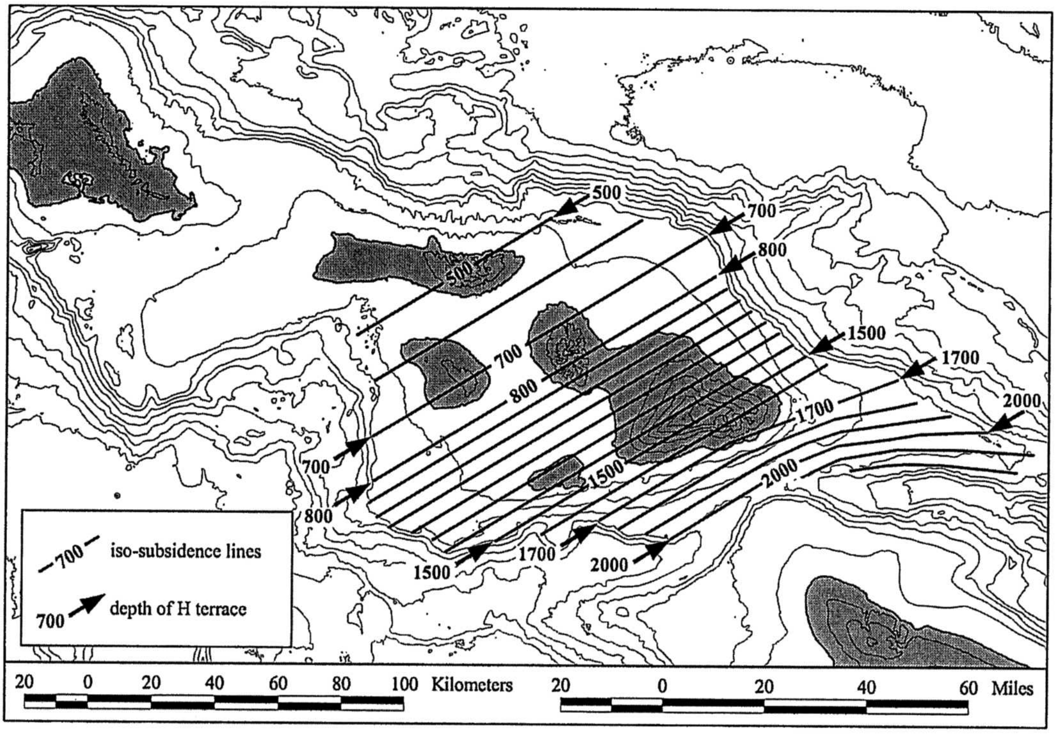

FIGURE 6. Estimated subsidence since 1.2 Ma. Contour interval is 500 m. Arrows show depth of H terrace at select locations. Solid lines indicate assumed amount of subsidence since the formation of the H terrace (iso-subsidence lines). For the Haleakalā ridge east of Maui, the direction and degree of tilt was determined from examination of submerged coral reefs that were originally horizontal (Moore et al. 1992).

is effectively restored to a horizontal feature at sea level, thus accurately reflecting the topography of Maui Nui at 1.2 Ma.

Within Maui Nui, different areas experience similar subsidence rates, though the timing of the sequence varies. The K terrace in the vicinity of East Moloka'i's summit and the H terrace in the vicinity of Haleakalā's summit have both subsided about 1500 m. Subsidence is essentially complete for East Maui, as evidenced by tide gauge measurements (Moore 1987), and for East Moloka'i, as evidenced by the small Kalaupapa Volcano, which has been essentially stable since its formation between 0.34 and 0.57 Ma (Clague et al. 1982). Therefore, a given volcanic summit in the Maui Nui complex appears to subside about 1500 m within about 1.2 myr of its shield formation, with older volcanoes completing subsidence earlier than younger ones. Under this assumption, the depth of the H terrace can be used to determine the changing rates of subsidence. The timing of shield completion and subsidence for East Maui, West Maui, and East Moloka'i varies, yet their summits can all be assumed to have subsided about 1500 m since formation. The depth of the H terrace differs near each summit, yet has a fixed age of 1.2 myr. Using differences in subsidence timing and amount near each summit, and an assumed subsidence stage 1.2 myr in duration, it is possible to calculate subsidence rates for three intervals: 2.3 mm/yr for the first 0.3 myr after the end of shield building, 1.0 mm/yr from 0.3 to 0.6 myr after shield building, and 0.8 mm/yr for the remaining 0.6 myr in the subsidence stage. The initial rate is comparable with the more reliable estimates from around the island of Hawai'i (2.4–2.6 mm/yr), with the

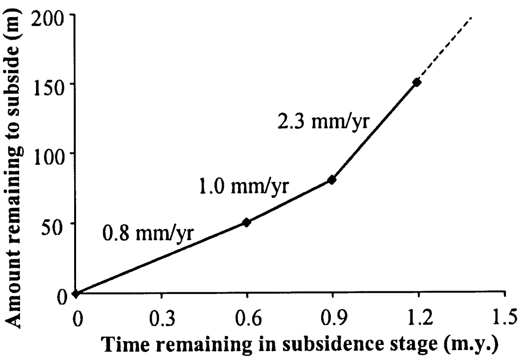

FIGURE 7. Subsidence rates/stages. The sequence here accounts for the changing rate of subsidence. Assuming that the Maui Nui complex has completed subsidence, the known amount of subsidence in the last 1.2 myr is essentially a measure of where a given point was in the subsidence sequence at that time. This was then used to determine the changing rate of the subsidence between 1.2 Ma and the present.

subsequent rates indicating that subsidence slows over time. These rates were compiled into the sequence shown in Figure 7. This sequence serves as a way to determine how the elevation at a location changes from that estimated for 1.2 Ma to that at present.

The amount of subsidence estimated to have occurred at a given location since 1.2 Ma (calculated for each location as the "subsidence amount grid") essentially marks where in the subsidence sequence the location was at that time. Assuming that each location experiences the same transition of rates with different timing, the sequence in Figure 7 indicates how a location transitioned from its position in the sequence at 1.2 Ma to its current position with subsidence complete. For example, areas that subsided 500 m since 1.2 Ma were assumed simply to subside at a rate of 0.83 mm/yr until reaching their current elevation with subsidence complete. On the other hand, locations that subsided 1500 m since 1.2 Ma were estimated to go through the sequence of rates in Figure 7, having just reached their current elevation after completing the subsidence sequence.

To account for subsidence, the adjusted DEM representing the appropriate amount of alkalic cap formation and erosion is determined for each point in time. A second adjustment for subsidence was made for each location based on (1) the point in time being considered, (2) that location's position in the subsidence sequence at 1.2 Ma, and (3) the sequence of rates from Figure 7. Between 1.2 Ma and the present, at intervals of 0.01 myr (10,000 yr) the appropriate adjusted DEM was adjusted further for the appropriate amount of subsidence; in total, 120 topographic models were calculated. These models incrementally transition from the presubsidence and prealkalic cap model for 1.2 Ma to the current topographic setting of completed subsidence and a fully formed and eroded alkalic cap.

Sea-Level Change

The extent of continental glaciation causes global sea level to fluctuate over time. The current interglacial sea stand is relatively high, but sea level was considerably lower than at present during the last glacial maximum around 20–21 ka (Fairbanks 1989). Sea-level change influenced the landscape of Maui Nui by changing its land area and by influencing when islands were connected or isolated. Actual sea level in the past is difficult to ascertain in a tectonically dynamic region such as Hawai'i. An approximation of sea level can be derived from oxygen isotope ratios in Foraminifera from seafloor sediment cores, which are largely a function of global ice volume and sea-surface temperature. The isotope record in Figure 8 is from Ocean Drilling Project (ODP) site 849 (Mix et al. 1995) and indicates the timing of major glacial and interglacial extremes. To avoid a false appearance of precision, the area of the Maui Nui complex was estimated for typical interglacial sea stands at current sea level and for typical glacial maximum sea stands at 120 m below present (an approximation within the range of estimates available) to show the minimum and maximum possible land area during a given period. Actual land area fluctuated between these two extremes according to the timing of glacial events. To estimate when islands were connected or isolated, the elevations of the saddles between

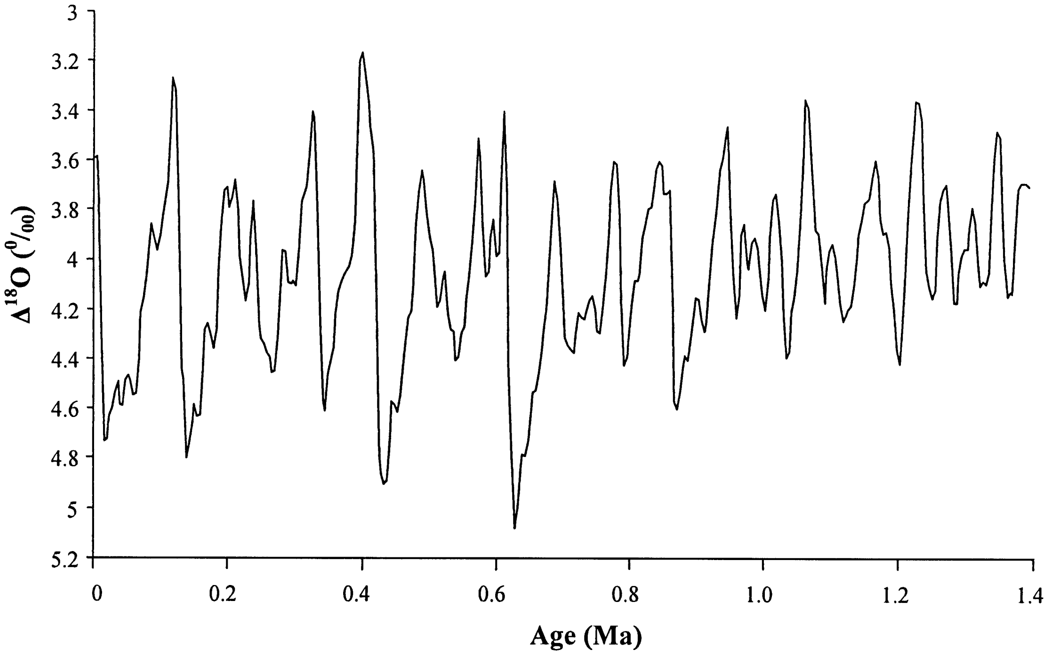

FIGURE 8. Timing of glacial cycles since 1.4 Ma. Oxygen isotope record for benthic Foraminifera in Ocean Drilling Project (ODP) core 849 from the eastern equatorial Pacific (Mix et al. 1995). Peaks represent periods with high sea levels comparable with present levels; low points indicate glacial periods when sea level was around 120 m lower. Given the many uncertainties of sea-level estimation, this serves as a way to determine the approximate timing of major sea-level changes over the given period.

volcanoes, which lowered as subsidence ensued, were examined in the context of likely sea levels associated with the timing of events in Figure 8.

RESULTS

Maui Nui Complex before 1.2 Ma

Because Haleakalā Volcano overlies much of the original shield surfaces of older volcanoes in the Maui Nui complex, the topographic history of the complex before Haleakalā's formation is speculative. Penguin Bank, the oldest volcano in the Maui Nui complex, was connected to O'ahu when it originally formed (Carson and Clague 1995). Taking into account the depth of the break-in-slope associated with Penguin Bank (1100 m), indicating the amount of subsidence since its formation, and the depth of the saddle between Penguin Bank and O'ahu's Ko'olau Volcano (600 m), the saddle was probably about 500 m above sea level at its maximum around 2.2 Ma. In addition, West Moloka'i's break-in-slope (W terrace) extends west to O'ahu, indicating that when it formed around 2.0 Ma it was also connected. There was a broad plain connecting O'ahu and West Moloka'i, though the elevation of the saddle connecting them was perhaps only 200 m at its maximum. The resulting island (which might appropriately be called "O'ahu Nui") had an area probably in excess of 7000 km^2. Given the maximum elevations of the saddles and probable rates of subsidence when these features formed (at least 2.0 mm/yr), the Penguin Bank–O'ahu saddle probably submerged around 2.0 Ma, and the West Moloka'i–O'ahu saddle perhaps 1.9 Ma. Thus, the O'ahu–Maui Nui connection probably lasted only 0.3 myr or so.

By the time East Moloka'i completed its shield building at 1.8 Ma, Maui Nui was a

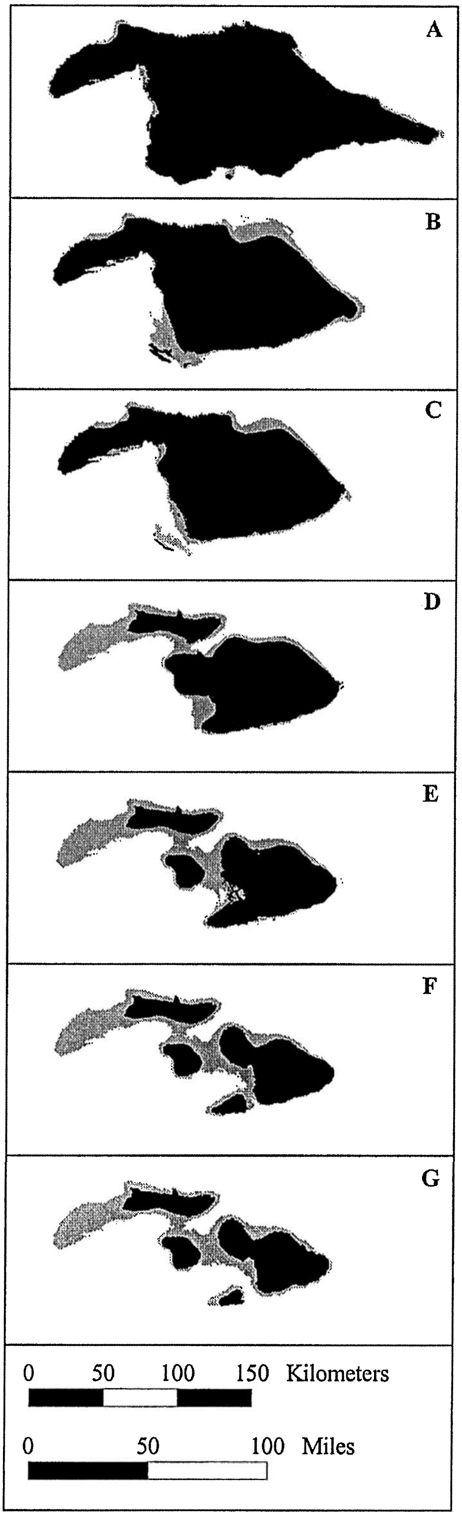

FIGURE 9. Summary of Maui Nui history. For each 0.2-myr interval, the approximate range of variation in the area and configuration of islands around that time is summarized. Black shading represents land area during high sea stands of interglacial periods, gray shading represents area during low sea stands of glacial periods. *A*, Around 1.2 Ma: single landmass; 14,000–14,600 km^2; Haleakalā about 3500 m. *B*, Around 1.0 Ma: single landmass; 9800–11,400 km^2; Haleakalā about 3500 m. *C*, Around 0.8 Ma: single landmass; 7100–9000 km^2; Haleakalā about 3500 m. *D*, Around 0.6 Ma: single landmass during low sea stands, two landmasses during high sea stands; 5500–7700 km^2; Haleakalā about 3500 m. *E*, Around 0.4 Ma: single landmass during low sea stands, three landmasses during high sea stands; 4200–6800 km^2; Haleakalā about 3500 m. *F*, Around 0.2 Ma: single landmass during low sea stands, four landmasses during high sea stands; 3400–6100 km^2; Haleakalā about 3400 m. *G*, Last glacial cycle: two landmasses during low sea stands, four landmasses during high sea stands; 3100–5900 km^2; Haleakalā about 3000 m.

distinct island consisting of three fully formed volcanoes (Penguin Bank, West Moloka'i, and East Moloka'i), with West Maui and Lāna'i Volcanoes probably in their early shield-building stages. Even after the massive landslide on East Moloka'i's north flank, this island was probably larger than 5000 km^2, with East Moloka'i rising to a summit of about 3000 m. Gradually, Lāna'i, West Maui, East Maui (Haleakalā), and Kaho'olawe Volcanoes formed as the older volcanoes in the complex subsided. By the time Haleakalā Volcano finished shield building around 1.2 Ma, Maui Nui was at its maximum size.

Area of the Maui Nui Complex

The changing area of the Maui Nui complex since its maximum extent is summarized in Figure 9. Both a higher estimate assuming a glacial-period low sea stand and a lower estimate assuming an interglacial-period high sea stand are shown. Penguin Bank is overlain by a thick coral cap about 500 km^2 in extent, which formed gradually over a shield whose original topography is unknown; therefore, Maui Nui's area before the formation of the coral may be overestimated by as much as 500 km^2. Maui Nui's area at its maximum extent (around 14,000 km^2) exceeded that of the current "Big Island" of Hawai'i (10,458 km^2).

As the Maui Nui complex subsided over the past 1.2 myr, its area diminished greatly, despite some fluctuation with sea-level changes. It is likely that the current four islands compose the smallest area (3037 km^2) that the Maui Nui complex has occupied in the last 2 myr. Even during the last glacial maximum (as recently as 20–21 ka), Maui Nui's area (5900 km^2) was nearly twice what it is currently.

Timing of Separation

Islands are isolated when the saddle between two volcanoes is submerged by subsidence and/or rising sea level. By accounting for these processes, the topographic models produce rough estimates of when Maui Nui isolation events occurred. Since 1.2 Ma, the first connection to be submerged was that between West Moloka'i and Penguin Bank, probably over 1 Ma, but this reconnected repeatedly during low sea stands, particularly as the coral platform approached its current extent. East Moloka'i and West Maui developed a permanent embayment between them perhaps around 0.7 Ma, but both remained connected via Lāna'i as recently as the last glacial maximum. The saddle between East Moloka'i and Lāna'i first submerged around 0.6 Ma but reemerged during glacial periods since that time. Similarly, the saddle between Lāna'i and West Maui submerged around 0.4 Ma and has reemerged during glacial periods. The isthmus between East and West Maui has probably remained emergent since Haleakalā's formation: no sea stand has been high enough in recent history to submerge it, and it has been experiencing subsidence that has probably slowed only recently. Therefore its elevation relative to sea level is probably now as low as it has ever been. The saddle between East Maui and Kaho'olawe probably first submerged around 0.2 Ma. Although it may have reconnected during the penultimate glacial maximum around 150 ka, it has subsided enough so that during the last glacial maximum Kaho'olawe was not connected to the other Maui Nui islands.

Viewing the topographic models in the context of probable sea levels, it appears that over the last 1.2 myr all four of the Maui Nui islands have been connected into a single landmass more than 75% of the time. The Maui Nui complex comprised substantially separate islands between five and seven times (during interglacial periods), though these were all fairly recent, occurring in the last 0.6 myr, and were minimal in duration, lasting only 0.05 myr (50 kyr) at most. The current configuration of four separate islands is therefore an unusual state in the context of the last 1.2 myr. These results differ somewhat from those of Carson and Clague (1995) discussed earlier because their analysis was speculative and did not entail a quantitative spatial model like the one presented here. The most substantial differences are that the ages of initial isolation given here are somewhat older than those of Carson and Clague and that recent connections involving sea level are considered in detail in this model.

Topography

The topography of Maui Nui at its maximum extent (around 1.2 Ma) differed greatly from that of Hawai'i (Figure 10). Maui Nui had much more lowland below 1000 m than Hawai'i (77% compared with 49%), suggesting that Maui Nui's climate at that time differed from Hawai'i's. Even after subsidence was essentially complete, during low sea stands of recent glacial periods, 90% of Maui Nui's area was below 1000 m, as compared with 85% at present. Therefore the Maui Nui complex has been composed of extensive contiguous lowlands with less extensive and more isolated uplands.

The detail of the model in the vicinity of Haleakalā's summit allows a fairly accurate reconstruction of its elevation over time. Considering the amount of subsidence estimated to have occurred in the summit region (1500 m) and the current elevation of the original volcanic shield summit (about 2000 m), Haleakalā's height at the completion of shield building was probably in the vicinity of 3500 m. This is considerably less than the estimate of 5000 m (Moore and Clague 1992), which did not account for the timing of alkalic cap formation or the spatial varia-

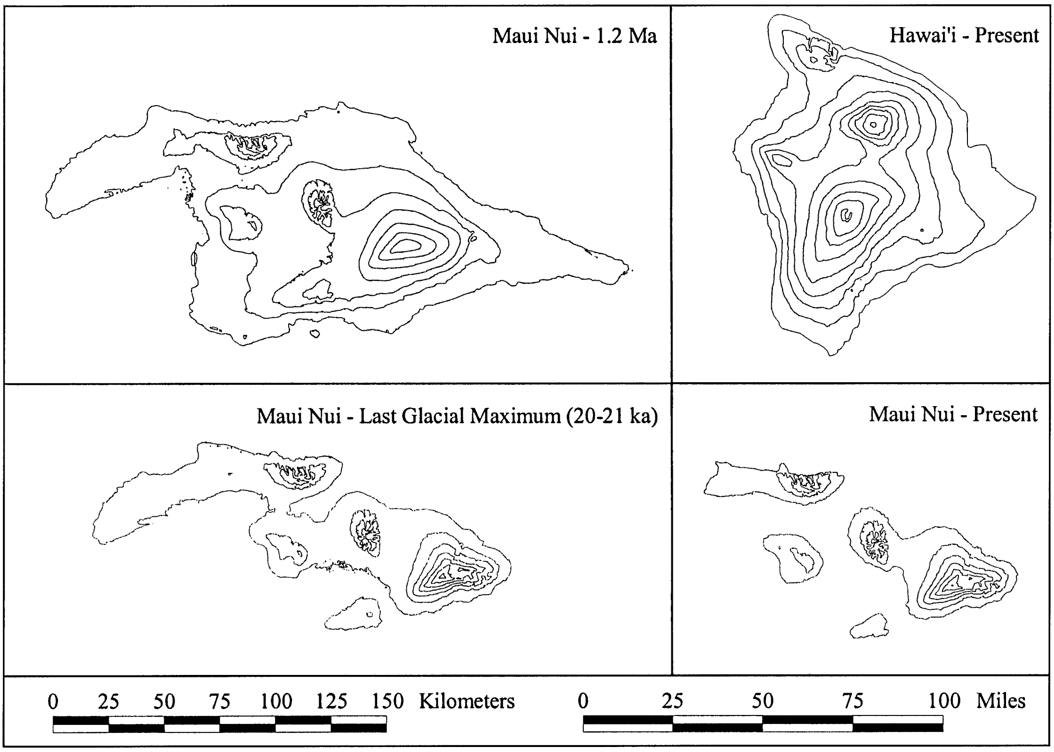

FIGURE 10. Topography of Maui Nui and Hawaiʻi. Contour interval 500 m. Maui Nui's topography shown at maximum extent, at the last glacial maximum, and at present. Current topography of Hawaiʻi shown for comparison.

tion in subsidence. As subsidence occurred, the alkalic cap was added to the summit; because these rates were roughly comparable, the summit elevation probably did not change greatly while the alkalic cap was being formed. Considering fluctuations of sea level and the episodic nature of the alkalic cap formation, the summit elevation probably varied between 3300 and 3700 m from 1.2 to 0.4 Ma. After that, the summit lowered to its current height only in the last 0.15 myr as it eroded.

DISCUSSION

Climate

With more lowland area, Maui Nui at its maximum extent probably had more land area in warmer temperature regimes than the current island of Hawaiʻi, which has large areas of cooler montane, subalpine, and alpine climates. For the current interglacial climate, the dominant feature of Hawaiian climates is northeasterly trade winds that deposit high amounts of rainfall on windward mountain slopes, leaving leeward slopes relatively dry (Giambelluca and Schroeder 1998). Because the saddles between Maui Nui volcanoes were lower than those currently on Hawaiʻi, trade wind–driven orographic rainfall may have formed a somewhat discontinuous rainforest belt on Maui Nui's windward slopes, gradually becoming more patchy as the saddles subsided to their current positions near sea level. It is also likely that Maui Nui was large enough to generate localized land-sea orographic rainfall as occurs today on the island of Hawaiʻi; on the west and southeast slopes of Mauna Loa, where trade winds are blocked, heating of the land surface draws moisture-laden air up the slopes of the mountain, generating convectional rainfall that is sufficient to create a rain-forest climate in those otherwise leeward regions (Giambelluca and Schroeder 1998). Maui Nui probably also had such leeward rain-forest regions on the south and west slopes of the island.

It is unclear how Maui Nui's topography at its maximum extent would have influenced climate during glacial periods. Gavenda (1992) summarized evidence for Hawaiian paleoclimates and concluded that glacial periods were generally cooler and wetter than at present. Recent palynological work by Hotchkiss (1998) and Hotchkiss and Juvik (1999) indicated that during glacial periods, trade wind inversion (the top of the cloud layer and thus the upper limit of rain forest) lowered considerably, in association with widespread cooling of 3–5°C. In addition, a general weakening of trade winds and/or decrease in moisture capacity of the associated air mass resulted in generally drier conditions than present for areas that are currently in trade wind rain-forest regions, suggesting reduced rain-forest area. Influence of these changes on convectional rainfall is uncertain. Maui Nui's greater area at its maximum extent, coupled with weaker trade winds, may have allowed more uneven heating and thus greater convectional rainfall; however, decreased temperature and lower moisture content in air masses may have diminished this type of precipitation.

During recent glacial periods, the Maui Nui complex had topography similar to that at present but included an extensive lowland between major volcanoes that is not present today. The resulting difference may have had little influence on trade wind–generated precipitation, though this was likely diminished, as discussed earlier. There may have been some convectional precipitation due to diminished trade winds and greater land area available for heating, although again it is unclear how glacial climates influenced this type of precipitation. However, with glacial-period climates generally drier, and with discontinuous mountain masses for orographic uplift, the lowland area connecting the volcanoes of the Maui Nui complex probably had a relatively dry climate at that time. Therefore, at least for the past 0.5 myr or so, the rain-forest regions of the Maui Nui complex have likely been discontinuous and more arid climate regions may have been more contiguous and extensive, particularly during low sea stands of glacial periods when islands were connected.

Estimates of Haleakalā's summit elevation can be used to address speculation about the potential for glacier formation on Haleakalā. Porter (1979) estimated that an ice cap on Mauna Kea (with a summit elevation of 4206 m) extended down to 3200 m and calculated an equilibrium line altitude (ELA) at an elevation over 3700 m; above that elevation there was net accumulation and below it there was net ablation, with the presence of ice below the ELA a function of glacier flow. Moore et al. (1993) speculated that Haleakalā was high enough before about 0.3 Ma to have supported glacial ice and suggested that the crater formed by glacial outburst floods; they assumed a maximum elevation of 5000 m, however, and suggested that the crater formed early in the postshield history (before subsidence). Because Haleakalā's elevation appears not to have substantially (if ever) exceeded 3700 m, there would have been little net ice accumulation under conditions similar to those of the last glacial period. Because it had subsided to well below that elevation by the time the crater is now believed to have formed, it is unlikely that outwash from multiple glaciations formed the Haleakalā Crater.

Biogeography

The most obvious biological consequence of Maui Nui's history is that the dispersal of species into and within the complex was greatly facilitated. With direct connections to O'ahu early in its history, species (even flightless or poorly dispersed species) dispersed easily from older to younger volcanoes. Subsequent connections between Maui Nui islands further facilitated dispersal until very recently. Flightless birds appear to have made use of connections in at least two cases. First, the flightless waterfowl, or Moa nalos

(Anatidae), in the genus *Thambetochen* may have dispersed from O'ahu to Maui Nui via the Penguin Bank land bridge and then throughout Maui Nui via subsequent connections (Sorenson et al. 1999). Hawaiian flightless ibises (*Apteribis* spp.) are restricted to Maui Nui; because ibises show little tendency to become flightless (only one other instance is known), it is likely that they developed flightlessness on Maui Nui, resulting in a vicariant distribution as the landmass became separate islands (Olson and James 1991).

Maui Nui's considerable size and probable range of environments also presented a substantial target for the overwater dispersal of species, not only for species dispersing from older islands but also from outside the Hawaiian Islands. Lowrey (1995) estimated that 11 species of *Tetramolopium* (Asteraceae) evolved from a common ancestor that colonized Maui Nui around 0.6 to 0.7 Ma. The ancestors are believed to be from cool climates of the New Guinea highlands, so Maui Nui would have been the most likely point of colonization because it had the most extensive high-elevation habitats in the Hawaiian Islands at that time.

In the past, Maui Nui was closer to other islands than it is at present, which likely made it more of a target and a source of dispersal than is apparent. When the oldest volcanoes of Hawai'i Island completed their shield building around 0.5–0.6 Ma, the shoreline associated with the M terrace would have been less than 15 km from Maui Nui's shoreline. This distance is comparable with that currently between Maui Nui islands and is considerably less than the current distance between Maui and Hawai'i (nearly 50 km). Similarly, the distance between Maui Nui and O'ahu was much closer during low sea stands, even as recently as the last glacial period. With Penguin Bank exposed, Maui Nui was about 14 km from O'ahu, much less than the current distance between O'ahu and Moloka'i (40 km).

Maui Nui's history probably played an important role in speciation. Because larger islands have been shown to experience more speciation than small ones (Heaney 1986, Losos and Schluter 1999), Maui Nui's area through evolutionary time may be more relevant to the evolution of diversity than the current size of its constituent islands. Further, the process of islands splitting up may produce vicariant speciation through the formation of a barrier (Mayr 1963), in this case a water channel or inhospitable lowland. With the isolation process repeated with iterations of sea-level fluctuation and associated climate change, numerous isolation scenarios may have been possible; however, iterative speciation involving glacial cycles is probably uncommon (Joseph et al. 1995). In addition to the two examples of flightless birds previously mentioned, vicariant speciation has been suggested within several lineages, as summarized by Funk and Wagner (1995): true bugs in the genus *Sarona* (Miridae) (Asquith 1995), plants in the genus *Schiedea* (Caryophyllaceae) (Wagner et al. 1995), and spiders in the genus *Tetragnatha* (Tetragnathidae) (Gillespie and Croom 1995). Liebherr (1997) proposed a more complex vicariance scenario in a phylogeny of several genera of beetles (Carabidae, tribe Platynini): several subclades include species from each of three volcanoes (East Moloka'i, East and West Maui), suggesting that initial divergence within Maui Nui was followed by parallel vicariance in the resulting sublineages.

Considering past island configurations and climates, the species composition of islands of the Maui Nui complex should differ from those of the other Hawaiian Islands in several ways. First, because of facilitated dispersal and enhanced speciation, Maui Nui islands should contain more species than would be predicted by their age and area alone. Second, because Maui Nui islands are part of a single "evolutionary isolate," they should share many species that are endemic to Maui Nui as a whole yet contain relatively few species that are endemic to only a single Maui Nui island. Finally, these patterns should be most pronounced in lowland and dry climates, because these have been spatially and temporally continuous over the lifetime of the Maui Nui complex. A detailed biogeographical analysis of the native angiosperm flora confirms many of these points (Price 2002). A high degree of floristic similarity, low-level single-island endemism, and high species richness (particularly in dry habitats) characterize the floras of the islands of the Maui Nui complex.

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